

Assessing spider diversity on the forest floor: expert knowledge beats systematic design

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Abstract. The design of sampling schemes affects the results of biodiversity inventories. As an approach for quantifying the implications of such effects, we compared data on spider communities sampled in a beech-dominated forest floor habitat by 1) a regular grid of pitfall traps (systematic design) and 2) an expert-based distribution of traps (stratified design). We tested whether the two designs would lead to similar conclusions about the diversity and composition of ground-dwelling spider communities. Estimates of species richness, rarefied species richness and activity density calculated per trap were significantly higher in the stratified than in the systematic design. The community composition based on the presence or absence of sampled species or based on log-transformed activity densities differed significantly. Most of the dissimilarity between the community estimates of the two designs was attributable to three species, with *Pardosa saltans* Töpfer-Hofmann 2000 being more common in traps of the stratified design and *Tenuiphantes zimmermanni* (Bertkau 1890) and *Walckenaeria cuspidata* Blackwall 1833 being more frequently observed in traps of the systematic design. Our study suggests that a stratified sampling design is better suited for inventory surveys of spider communities of forest-floor habitats, as trap locations of this design reflect specific habitat needs. It is important to note that inventories are a major field for the application of such designs and that greater care is needed for the application of inferential statistics. For example, the non-randomness that is caused by expert selection of sampling sites may violate fundamental assumptions of simple linear models.

Keywords: Araneae, biodiversity, inventory, expert-based sampling, regular sampling, sampling design

Biodiversity research provides crucial information for the development of conservation strategies (Brooks et al. 2004). Strict inventories that generate comprehensive taxonomic lists for a discrete spatiotemporal unit are thus prerequisites for protecting species richness (Longino & Colwell 1997). Moreover, reliable estimates of species composition are needed to enable researchers to monitor biodiversity changes successfully (Dorow et al. 1992; Colwell & Coddington 1994; Buckley & Roughgarden 2004). As a contribution to this issue, we compared estimates of diversity and species composition of ground-dwelling spiders in a forest-floor habitat of a beech forest with two different sampling designs (systematic vs. stratified; e.g., Southwood & Henderson 2000).

Systematic designs that are based on a regular distribution of sampling locations in a study area (Woodcock 2005) are a common approach in diversity surveys (e.g., sampling transects for flower-visiting insects: Rundlöf et al. 2008). However, such a design depends on a priori decisions on the distance between sampling points in relation to the scale of environmental heterogeneity and the mobility of the focal taxa. A regular placement of sampling locations further assumes that environmental gradients which affect the analysed taxa are constant over the study area and do not vary over different spatial scales (Quinn & Keough 2002). Systematic designs may therefore be most appropriate for homogeneous habitats with weak or very simple environmental gradients. Dorow et al. (2007) suggested that stratified sampling of pre-defined subpopulations provides an appropriate alternative for biodiversity inventories, since it may improve precision by taking account of specific habitat types (see also Hayek & Buzas 1997). In stratified designs, specific microhabitats can be selected based on expert knowledge, and this approach may thus provide a more precise

estimate of diversity in heterogeneous study regions than random sampling (Southwood & Henderson 2000). In general, subjective selection of sampling locations biases analyses of ecological data by preconceptions of the investigator (Hirzel & Guisan 2002). However, subjectivity may be necessary and valid for certain research questions (McCune & Grace 2002). A strict inventory of species richness in heterogeneous habitats, for example, may only be reliable if the sampling design is biased by expert knowledge toward locations that support rare species and habitat specialists. An important assumption for using data from stratified designs is that information about the stratum is included as a predictor in statistical models (Quinn and Keough 2002). Comparative studies on the trade-offs between systematic and stratified designs are generally rare (Hirzel & Guisan 2002) and not available for invertebrate communities in temperate forests.

Our study focused on spiders, because this taxon forms a diverse group in temperate forests, and species are sensitive to environmental heterogeneity (Wunderlich & Blick 2006; Ziesche & Roth 2008; Birkhofer et al. 2010). Data were collected with pitfall traps in a 34.8 ha area for 16 months. The spatial arrangement of traps either followed a systematic design (regular grid) or a stratified design (expert-based selection of 14 pre-defined habitat structures). We hypothesize that the design based on expert knowledge would provide a more complete estimate of spider diversity than the systematic design based on a regular grid.

METHODS

Study site and sampling.—The study was conducted in the strict forest reserve “Locheiche” located in the National Park Kellerwald-Edersee in the northern part of Hesse, Germany

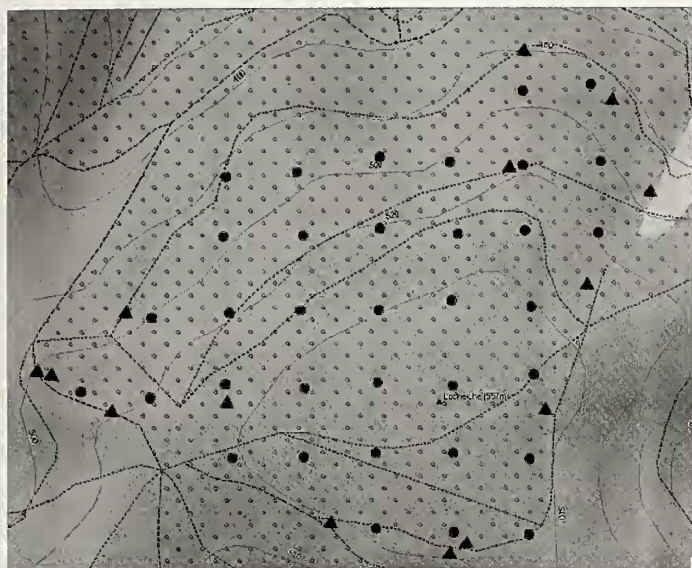


Figure 1.—Trap locations (points) in the 34.8 ha study area in the Kellerwald strict forest reserve “Locheiche” with the systematic design (circles, one trap per point) and the stratified design (triangles, three traps per point).

(480–555 m a.s.l.; 51°08′30.45″N, 08°59′21.82″E) as a part of the long term studies in the forest reserves of Hesse (Dorow et al. 2010). The forest has not been managed since 1988, and beech trees (*Fagus sylvatica* L.) of an age of 81–120 years grow on the north and west exposed slopes of the study area. Additional tree species are *Quercus petraea* (Mattuschka) Liebl., *Larix decidua* Mill., *Acer pseudoplatanus* L. and *Picea abies* (L.) H. Karst. The annual mean temperature is 7.6°C, and the average annual precipitation is 765 mm (www.naturwaelder.de). The soil type is a cambisol with a pH of 5.1 in the uppermost horizon (Harmonized World Soil Database 2009).

In total, 77 funnel pitfall traps (diameter 10 cm, filled with approximately 200 ml of 70% ethanol and 99.5% glycerin at a

ratio of 2:1) were placed on the forest floor (for details see Dorow et al. 1992). Thirty-five traps were arranged in a regular grid with an inter-trap distance of 100 m (systematic design, referred to as SYS below: Fig. 1), and 14 triplets of traps (42 traps in total) were placed at pre-defined locations with a distance of 5 m between traps in a triplet (stratified design, referred to as STR below: Fig. 1, Table 1). We account for these differences in inter-trap distances within and between designs in our analyses (see statistical analysis). Forest inventory points at 100×100 m grid intersections were established on the forest floor, and pitfall traps of the systematic design were placed next to these standardized locations. Locations of the traps in the stratified design were defined based on an inspection of the study area and structures outlined in Table 1. Traps were open for 16 months (29 October 2008 to 23 March 2010) and were emptied every 4 weeks. In winter, traps were not emptied before spring due to snow cover from 11 December 2008 to 25 March 2009 and from 25 November 2009 to 23 March 2010. Spiders were determined using standard keys (Roberts 1987, 1995; Nentwig et al. 2013), and the nomenclature followed Platnick (2013). Juveniles were only identified to the family level and were not included in the analysis.

Statistical analysis.—Before analyses commenced diversity metrics were corrected for differences in sampling effort between designs (systematic: 35 traps vs. stratified: 42 traps) by using the following approach. Traditional diversity metrics, such as species richness (including species richness that was rarefied to a minimum of 24 individuals observed in one trap), activity density or the inverse Simpson index were calculated as means per trap over the 16 month study period and are presented as average values per trap. As the capture probability of pitfall traps varies with both activity and density of the species, the term activity density should be used (Heydemann 1957). To make the results more intuitive we used the inverse of the Simpson index instead of its original formulation, as an increase in the inverse index reflects an increase in diversity (Magurran 1988).

Table 1.—Description of trap locations in the stratified (1–14) and systematic design (201–235). Note that each location of the stratified design was sampled with three pitfall traps.

Trap ID	Description
1	Beech-spruce-larch forest with needle and leaf litter
2	Border of forest-driveway with <i>Avenella flexuosa</i>
3	Border of forest-driveway with grasses and <i>Urtica dioica</i>
4	Woodrush beech forest, underlayer without herb layer
5	Woodrush beech forest, stony hilltop
6	Dense beech young stands with maple
7	Charcoal pile with <i>Cardamine bulbifera</i>
8	Edge of the forest with several shrub species
9	Charcoal pile with grass and young beech stands
10	Glade with grass and young beech stands
11	Young spruce plantation
12	Mixed beech-oak-larch forest
13	Border of forest-driveway, stony, poor herb layer
14	Border of forest-driveway, with young stands of beech and larch
201–206, 208–224, 226, 227, 230–232, 235	Forest floor covered with beech litter, without herb layer
225, 228, 229, 233, 234	Forest floor covered with beech and needle litter, without herb layer
207	Forest floor with grass and young stands of beech

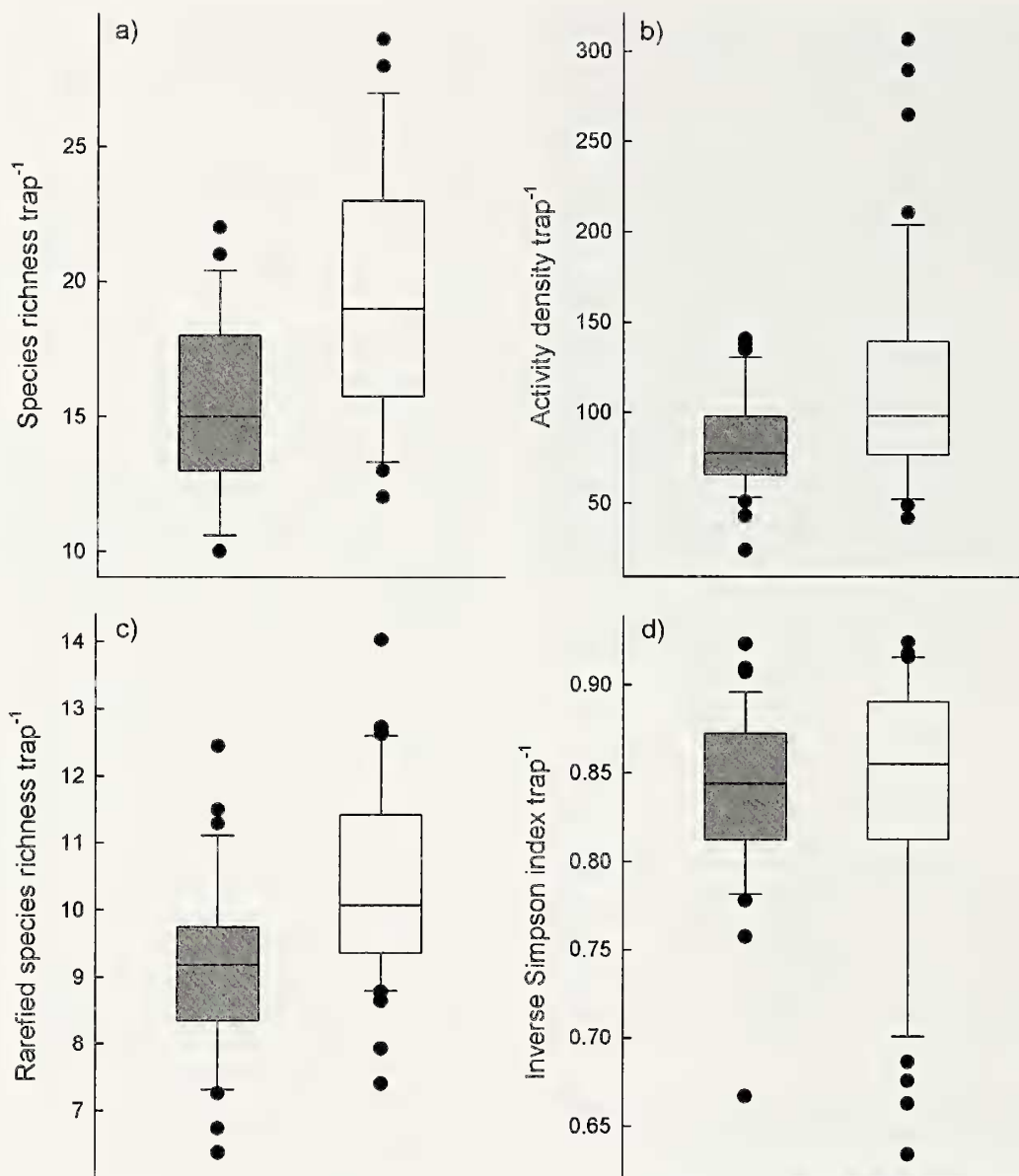


Figure 2.—Median, 75 and 95% quartiles and outliers for a) species richness, b) activity density, c) rarefied species richness ($n = 24$) and d) inverse Simpson index per pitfall trap for spider assemblages sampled in a systematic (SYS, gray) or stratified (STR, white) design.

Diversity and abundance metrics were compared between designs by one-way permutational analysis of variance with permutation of residuals under a reduced model and design (systematic vs. stratified) as fixed factor (PERMANOVA: Anderson 2001). We included X and Y coordinates of all trap locations as co-variables in our models to account for the fact that some traps within, but also between, designs were located more closely to each other. All univariate tests were based on Euclidean distances and 10,000 permutations. The univariate PERMANOVA based on Euclidean distances is analogous to a traditional one-way ANOVA, but P-values are obtained from permutations (Anderson and Millar 2004). We thus avoid the assumption of normality in our statistical models (e.g., Anderson et al. 2008) and show all results using box and whisker plots as recommended by Dytham (2003) for such data.

To assess the differences in community composition between sampling designs, we calculated resemblance matrices based on

Sørensen (presence or absence of species) or Bray-Curtis (log $x+1$ -transformed activity densities) distances between traps in both designs. We log-transformed activity density data to weigh down the contribution of abundant species to differences between the two designs and to emphasize the importance of rare species (Clarke et al. 2006). We used principal coordinate analysis (PCO) based on Bray-Curtis distances to visualize the dissimilarity of communities between traps from both designs (Clarke & Warwick 2001). To explore the individual contribution of species to dissimilarities between the two designs, we used similarity percentage analysis (SIMPER; Clarke & Warwick 2001). We further tested for homogeneity of multivariate dispersion by comparing the distances of communities per traps to group centroids between both designs (PERMDISP routine). All analyses were performed using PRIMER version 6.1.13 with the PERMANOVA + add-on version 1.0.3 (PRIMER-E, Plymouth, UK: Anderson et al. 2008).

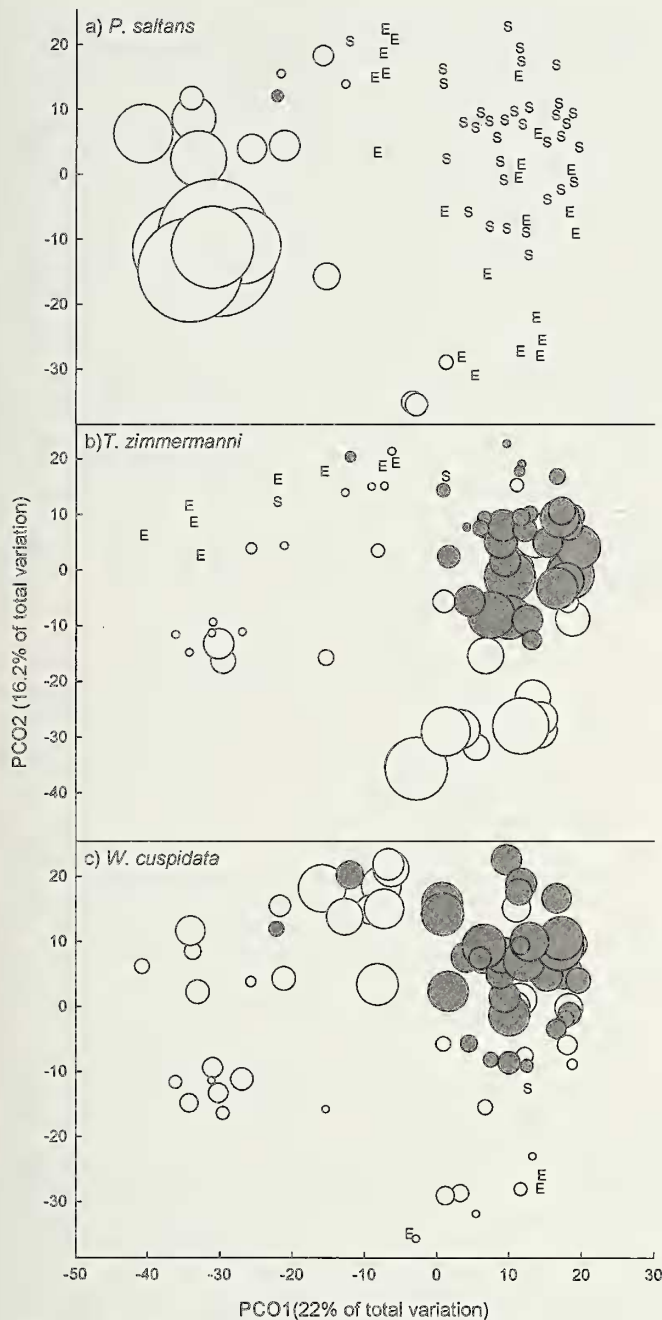


Figure 3.—Principal coordinates analysis based on Bray-Curtis similarities of log-transformed activity density data from all traps. The size of the bubbles corresponds to the number of individuals sampled in each pitfall trap in the systematic (SYS, gray) or stratified (STR, white) design for a) *Pardosa saltans* (bubble size range: 1–173 individuals), b) *Tenuiphantes zimmermanni* (1–62 individuals) and c) *Walckenaeria cuspidata* (1–39 individuals). Letters stand for traps that did not contain any individuals from the species in the stratified (expert-based, E) or systematic (S) sampling. Note that bubbles may overlap.

RESULTS

In total, 8012 adult spiders were sampled from 96 species in 14 families (see Appendix 1). Traps in the STR design contained 90 species, of which 42 were exclusively found in the STR design. Traps of the SYS design contained 54 species, of which 6 were exclusively found in the SYS design. Species

richness (pseudo- $F_{1,74} = 31.59$, $P < 0.001$) and activity density (pseudo- $F_{1,74} = 13.99$, $P < 0.001$) per trap were significantly lower in the SYS than in the STR design (Figs. 2a,b). Rarefied species richness was also significantly lower in the SYS design (Fig. 2c; pseudo- $F_{1,74} = 17.18$, $P < 0.001$). The inverse Simpson index did not differ significantly between designs (Fig. 2d; pseudo- $F_{1,74} = 1.10$, $P = 0.301$).

Community composition based on the presence or absence of species in traps (Sørensen similarity, pseudo- $F_{1,74} = 7.04$, $P < 0.001$) or based on log-transformed activity densities (Fig. 3, Bray-Curtis similarity, pseudo- $F_{1,75} = 8.02$, $P < 0.001$) differed significantly between the two designs. Although both designs shared 47 out of 96 species, similarity percentage analyses indicated that three common species contributed most to the significant dissimilarity between communities (Fig. 3). *Pardosa saltans* Töpfer-Hofmann 2000 was more common in traps of the STR design (mean abundance of 51 individuals across all traps) and almost absent from the SYS design (only two individuals were collected in one trap of the systematic design). In contrast, *Tenuiphantes zimmermanni* (Bertkau 1890) and *Walckenaeria cuspidata* Blackwall 1833 were more frequently observed in traps of the SYS design. In general, the multivariate dispersion of community composition was significantly smaller in the SYS design, indicating that community composition varied less between traps than in the STR design (PERMDISP; $F_{1,75} = 49.18$, $P < 0.001$).

DISCUSSION

Our study suggests that the stratified design provides a more representative estimate of diversity and a more comprehensive summary of community composition in the study area than a systematic design. Species richness was higher in the stratified design, and the number of exclusive species only sampled with this design was almost an order of magnitude higher than for the systematic design. However, expert knowledge is needed to select sample locations in stratified designs in order to sample all relevant microhabitats. In contrast, systematic designs do not require such knowledge, but decisions about the extent of the sampling area, the number of sample points and the inter-point distances also require a priori assumptions.

It has been previously suggested that systematic designs may not adequately represent the composition of communities, since environmental gradients that acted on the mammal species studied were not covered (Read et al. 1988; Pearson & Ruggiero 2003). The effectiveness of stratified methods to sample rare species in heterogeneous habitats was also highlighted for plant communities in coastal wetlands (Croft & Chow-Fraser 2009). In our study, the number of unique spider species was seven times higher in the stratified design, even though the same sampling technique was used and the survey lasted over the same period (16 months). Differences between designs were attributed to some common spider species; for example, *P. saltans* was predominantly collected by traps in the stratified design. This pattern highlights preferences of *P. saltans* for particular forest habitats (e.g., Hendrickx et al. 2001) that were only sampled in the stratified design. This observation also demonstrates the danger of missing specific habitat types if trap locations are arranged in a regular grid that is related to the number, size and distribution of habitats in the study area.

Tenuiphantes zimmermanni and *W. cuspidata* were more frequently observed in traps of the systematic design, but both species were also present at particular locations of the stratified design. This pattern reflects the rather broad habitat preferences of these two sheet-web weavers.

Community composition of spiders in individual traps was significantly more homogeneous in the systematic design than in the stratified design, reflecting a more diverse range of microhabitats sampled in the stratified design. The vast majority of Central European beech forests consist of a relatively uniform stand of dense beech trees without a shrub and herb layer (Standovár & Kenderes 2003; Gálhidy et al. 2006). These areas are interspersed by small patches of different structure (e.g., wayside herbs, seepage springs, glades, rocks). To cover such elements in a systematic design requires an enormous effort and resources that may not be available for biodiversity inventories. Although the study presented here clearly illustrates that a stratified sampling design is more efficient than a systematic design, we acknowledge that the observed differences may be limited to the study location. Thus additional studies are needed to confirm our results for other habitats in general.

To conclude, our results suggest that forest surveys aiming at strict inventories of ground-active arthropods should not be based on systematic designs even in moderately heterogeneous study areas. That approach is more expensive and provides a less precise estimate of diversity and community composition. We propose, instead, that stratified designs should be used for strict inventories in European forests if expert knowledge is available and that the use of systematic designs should be reserved for spatial analyses (e.g., Birkhofer et al. 2011; Sereda et al. 2012) or surveys in more homogeneous habitats (e.g., Diekötter et al. 2010). It is important to note that inventories are a major field for the application of such designs and that greater care is needed for the application of inferential statistics. For example, the non-randomness that is caused by expert selection of sampling sites may violate fundamental assumptions of simple linear models.

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Appendix 1.—Species and number of individuals (juveniles excluded) sampled by the systematic (SYS) and the stratified (STR) approach.

Family/Species	SYS	STR
Agelenidae		
<i>Coelotes terrestris</i> (Wider 1834)	507	479
<i>Histopona torpida</i> (C. L. Koch 1837)	115	87
<i>Inermocoelotes inermis</i> (L. Koch 1855)	129	213
<i>Malthonica silvestris</i> (L. Koch 1872)	21	18
Amaurobiidae		
<i>Amaurobius fenestralis</i> (Ström 1768)	26	29
Clubionidae		
<i>Clubiona comta</i> C. L. Koch 1839	0	1
<i>C. reclusa</i> O. P.-Cambridge 1863	0	1
<i>C. terrestris</i> Westring 1851	1	6
Dictynidae		
<i>Cicurina cicur</i> (Fabricius 1793)	128	211
Dysderidae		
<i>Dysdera erythrina</i> (Walckenaer 1802)	0	1
<i>Harpactea hombergi</i> (Scopoli 1763)	0	8
Gnaphosidae		
<i>Drassodex lesserti</i> (Schenkel 1936)	0	2
<i>Haplodrassus signifer</i> (C. L. Koch 1839)	0	1
<i>H. silvestris</i> (Blackwall 1833)	1	16
<i>H. umbratilis</i> (L. Koch 1866)	0	1
<i>Micaria pulicaria</i> (Sundevall 1831)	0	2
<i>Zelotes clivicola</i> (L. Koch 1870)	0	17
<i>Z. erebeus</i> (Thorell 1871)	0	3
<i>Z. subterraneus</i> (C. L. Koch 1833)	0	128
Hahniidae		
<i>Halmia helveola</i> Simon 1875	3	7
<i>H. pusilla</i> C. L. Koch 1841	0	17
Linyphiidae		
<i>Agyneta conigera</i> (O. P.-Cambridge 1863)	0	1
<i>Asthenargus paganus</i> (Simon 1884)	0	2
<i>Bathyphantes gracilis</i> (Blackwall 1841)	0	1
<i>B. nigrinus</i> (Westring 1851)	0	1
<i>Bolyphantes alticeps</i> (Sundevall 1833)	0	5
<i>Ceptomerus brevivalvatus</i> Dahl 1912	1	0
<i>C. cavernarum</i> (L. Koch 1872)	2	66
<i>C. dilutus</i> (O. P.-Cambridge 1875)	54	167
<i>C. pabulator</i> (O. P.-Cambridge 1875)	1	48
<i>C. sylvaticus</i> (Blackwall 1841)	21	134

Appendix 1.—Continued.

Family/Species	SYS	STR
<i>Ceratinella brevis</i> (Wider 1834)	1	35
Linyphiidae		
<i>Dicymbium tibiale</i> (Blackwall 1836)	28	35
<i>Diplocephalus cristatus</i> (Blackwall 1833)	0	1
<i>D. latifrons</i> (O. P.-Cambridge 1863)	1	13
<i>D. picinus</i> (Blackwall 1841)	51	122
<i>Diplostyla concolor</i> (Wider 1834)	1	65
<i>Drapetisca socialis</i> (Sundevall 1833)	3	0
<i>Entelecara erythropus</i> (Westring 1851)	0	1
<i>Erigone atra</i> Blackwall 1833	0	1
<i>Formiphantes lepthyphantiformis</i> (Strand 1907)	0	1
<i>Gonatum rubellum</i> (Blackwall 1841)	26	40
<i>Helophora insignis</i> (Blackwall 1841)	0	42
<i>Jacksonella falconeri</i> (Jackson 1908)	8	0
<i>Lepthyphantes minutus</i> (Blackwall 1833)	0	1
<i>L. nodifer</i> Simon 1884	0	1
<i>Linyphia hortensis</i> Sundevall 1830	0	3
<i>Macrargus rufus</i> (Wider 1834)	36	34
<i>Maso sundevalli</i> (Westring 1851)	0	2
<i>Micrargus herbigradus</i> (Blackwall 1854)	26	130
<i>Microneta viaria</i> (Blackwall 1841)	36	26
<i>Monocephalus fuscipes</i> (Blackwall 1836)	0	1
<i>Neriene clathrata</i> (Sundevall 1830)	1	1
<i>N. emphana</i> (Walckenaer 1841)	1	0
<i>Nusoncus nasutus</i> (Schenkel 1925)	1	1
<i>Obscuriphantes obscurus</i> (Blackwall 1841)	0	1
<i>Palliduphantes pallidus</i> (O. P.-Cambridge 1871)	1	3
<i>Pocadicnemis pumila</i> (Blackwall 1841)	0	1
<i>Porrhomma campbelli</i> F. O. P.-Cambridge 1894	4	1
<i>P. pallidum</i> Jackson 1913	7	13
<i>Pseudocarorita thaleri</i> (Saaristo 1971)	4	3
<i>Saloca diceros</i> (O. P.-Cambridge 1871)	26	64
<i>Tapinocyba insecta</i> (L. Koch 1869)	327	256
<i>T. pallens</i> (O. P.-Cambridge 1872)	64	161
<i>T. praecox</i> (O. P.-Cambridge 1873)	0	1
<i>Tenuiphantes alacris</i> (Blackwall 1853)	4	2
<i>T. cristatus</i> (Menge 1866)	1	15
<i>T. flavipes</i> (Blackwall 1854)	10	73
<i>T. mendei</i> (Kulczyński 1887)	4	12
<i>T. tenebricola</i> (Wider 1834)	1	34
<i>T. tennis</i> (Blackwall 1852)	0	7
<i>T. zimmermanni</i> (Bertkau 1890)	443	487
<i>Thyreosthenius parasiticus</i> (Westring 1851)	1	0
<i>Walckenaeria acuminata</i> Blackwall 1833	0	11
<i>W. corniculans</i> (O. P.-Cambridge 1875)	24	45
Linyphiidae		
<i>W. cucullata</i> (C. L. Koch 1836)	47	111
<i>W. cuspidata</i> Blackwall 1833	566	407
<i>W. dysderoides</i> (Wider 1834)	8	7
<i>W. mitrata</i> (Menge 1868)	0	1
<i>W. obrusa</i> Blackwall 1836	4	14
Liocranidae		
<i>Agroeca brunnea</i> (Blackwall 1833)	0	4
<i>Apostenus fuscus</i> Westring 1851	0	2
Lycosidae		
<i>Alopecosa pulverulenta</i> (Clerck 1757)	0	12
<i>Pardosa amentata</i> (Clerck 1757)	0	1
<i>P. pullata</i> (Clerck 1757)	0	1
<i>P. lugubris</i> (Walckenaer 1802)	0	45
<i>P. saltans</i> Töpfer-Hofmann 2000	2	1018

Appendix 1.—Continued.

Family/Species	SYS	STR
<i>Trochosa terricola</i> Thorell 1856	2	75
<i>Xerolycosa nemoralis</i> (Westring 1861)	0	1
Salticidae		
<i>Euophrys frontalis</i> (Walckenaer 1802)	0	3
<i>Neon reticulatus</i> (Blackwall 1853)	9	9
Segestriidae		
<i>Segestria senoculata</i> (Linnaeus 1758)	0	3
Tetragnathidae		
<i>Metellina segmentata</i> (Clerck 1757)	1	0
<i>Pachygnatha degeeri</i> Sundevall 1830	3	1
Theridiidae		
<i>Robertus lividus</i> (Blackwall 1836)	33	41
<i>R. scoticus</i> Jackson 1914	7	4
Total:	2833	5179